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Differences of soil CO_2 flux in two contrasting subalpine ecosystems on the eastern edge of the Qinghai-Tibetan Plateau: A four-year study

Min Duan[a], Andi Li[b], Yanhong Wu[b], Zuoping Zhao[c], Changhui Peng[a], Thomas H. DeLuca[d], Shouqin Sun[b,*]

[a] Centre for Ecological Forecasting and Global Change, College of Forestry, Northwest A&F University, Yangling, 712100, China
[b] Key Laboratory of Mountain Surface Processes and Ecological Regulation, Institute of Mountain Hazards and Environment, Chinese Academy of Sciences, Chengdu, 610041, China
[c] College of Chemical and Environment Science, Shaanxi University of Technology, Hanzhong, 723000, China
[d] College of Forestry and Conservation, University of Montana, Missoula, MT, 59812, USA

A R T I C L E I N F O

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A B S T R A C T

Alpine and subalpine ecosystems on Qinghai-Tibetan Plateau are rich in soil organic carbon and are among the most sensitive regions to climate change, while little is known about the dynamics of soil carbon dioxide (CO_2) in alpine/subalpine ecosystems except for the grassland on the plateau. In this study, the monthly and inter-annual variations in soil CO_2 emission from a subalpine coniferous forest and a subalpine shrubland ecosystem on the eastern edge of the Qinghai-Tibetan Plateau were investigated from 2012 to 2015 using the opaque steady-state chamber method. Soil CO_2 flux rate during the growing season ranged from 153.3 to 683.6 mg m^{-2} h^{-1} in the coniferous forest, being twice of that (76.6–347.3 mg m^{-2} h^{-1}) in the shrubland, due to the elevation-induced differences in soil temperature and water content and the vegetation-induced differences in soil carbon and nitrogen pools. Both ecosystems showed large monthly variations in soil CO_2 flux rate, while relative to the coniferous forest, the shrubland had a less inter-annual variation in soil CO_2 emission. The two ecosystems had the same temperature sensitivity of soil CO_2 emission, which suggests that they will respond similarly to global warming concerning soil CO_2 flux rate. The results highlight the importance of soil CO_2 emission in subalpine forest and shrubland ecosystems, which can be helpful to reduce the uncertainty of regional estimates of carbon budget in subalpine regions under global warming.

1. Introduction

Combustion of fossil fuels and shifts in land use are known to be responsible for a significant amount of increased concentrations of carbon dioxide (CO_2) and other greenhouse gases (GHG) in the atmosphere (IPCC, 2013). According to the fifth assessment report of IPCC, these increases of GHG in the atmosphere will increase global average temperature by 0.3–4.8 °C in 2100 and this increase will be more prominent in high elevation and latitude regions ((IPCC, 2013; Pepin et al., 2015). Soils represent the largest single form of carbon (C) storage in terrestrial ecosystem and globally soils store more than twice as much C as the atmosphere with the annual C emission from the soil to atmosphere estimated around 80–98 Pg (Raich et al., 2002; Bond-Lamberty and Thomson, 2010; Budge et al., 2011). Soil CO_2 emission derived from plant and microbial physiological processes is regarded as the second-largest CO_2 flux to the atmosphere after terrestrial gross primary production (Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000; Bond-Lamberty and Thomson, 2010). Therefore, small changes in the magnitude of soil CO_2 emission could have a large influence on atmospheric CO_2 concentration and accurate estimates of soil CO_2 emission from different ecosystems can help effectively quantify terrestrial C storage.

Mountainous regions cover about 10% of the global land surface (Spehn and Körner, 2005), thus ecosystems in these areas play important roles in global C cycling (Li et al., 2016). Alpine soils accumulate large amounts of C and have very high organic C density due to low temperature in these regions (Schindlbacher et al., 2010; Yang et al., 2010; Budge et al., 2011). Conversely, studies predict that high altitude and latitude regions have a higher rate of temperature increase compared to their low-altitude or low-latitude counterparts (IPCC, 2013; Pepin et al., 2015). Biogeochemical processes such as the decomposition of soil organic matter (SOM) are highly temperature

* Corresponding author.
E-mail address: shouqinsun@imde.ac.cn (S. Sun).

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sensitive (Kirschbaum, 1995; Davidson and Janssens, 2006; Schindlbacher et al., 2010). Therefore, C cycling in alpine and subalpine ecosystems is uniquely vulnerable to climate change (Fu et al., 2006; Budge et al., 2011; Marcolla et al., 2011; Zhou et al., 2016). Understanding dynamics of CO_2 emission from these ecosystems and isolating environmental controls on CO_2 flux has become increasingly important in effectively predicting global C cycling in response to environmental change and adaptation to future climatic change (Marcolla et al., 2011; Li et al., 2016; Zhou et al., 2016).

Qinghai-Tibetan Plateau has been deemed as "earth's third pole", which has an average elevation over 3000 m and occupies a quarter of China's territory (Zheng et al., 2000; Li et al., 2006). The rate of warming in this region is about twice the observed global rate of warming with the temperature on the Qinghai-Tibetan Plateau increasing by 0.2 °C per decade over the past 50 years (Chen et al., 2013). Although studies have been conducted on C cycling and spatio-temporal pattern of CO_2 flux in alpine grassland and tundra ecosystems on the plateau (Kato et al., 2006; Chen et al., 2016; Zhao et al., 2017), to date, there is only limited data available to parameterize or validate CO_2 emission in subalpine forest (Lu and Cheng, 2009; Chen et al., 2014; Pang et al., 2016; Sun et al., 2017), especially in subalpine shrubland ecosystems (Zhao et al., 2006; Li et al., 2016; Sun et al., 2017), which covers 4.2% of the plateau (Zheng et al., 2000) and is the key vegetation type (transitional belts) between the alpine and subalpine forest and the tundra. The evaluation of CO_2 emission in subalpine shrubland along with forest ecosystems is important in exactly estimating regional C budgets and greatly increasing our comprehension of global C cycling in alpine and subalpine terrestrial ecosystems.

The objectives of this study were to: 1) Quantify soil CO_2 flux rates and investigate monthly and inter-annual variations of soil CO_2 emission in the subalpine coniferous forest and shrubland ecosystems on the eastern edge of the Qinghai-Tibetan Plateau; 2) Explore potential mechanisms underlying the differences of soil CO_2 emission between the two subalpine ecosystems. We hypothesized that the magnitude of soil CO_2 emission in the subalpine shrubland would be lower compared with that in the subalpine forest mainly because of lower soil temperature and soil water content induced by the higher elevation in the subalpine shrubland. This is the first attempt to compare soil CO_2 dynamics between subalpine forest and shrubland ecosystems, which can provide a more reasonable estimation of soil GHG emission from subalpine ecosystems.

2. Materials and methods

2.1. Study sites

This study was conducted in a subalpine coniferous forest (3065 m.a.s.l.) and a subalpine shrubland (3650 m.a.s.l.) ecosystem on the eastern slope of Gongga mountain (29º20‘–30º20′ N, 101º30‘–102º15′ E, 3000–3700 m.a.s.l.) in the southeastern fringe of the Qinghai-Tibetan Plateau. The climate in the region is typical montane temperate climate with cool summers. The mean growing-season (May to October) precipitation and temperature from 2012 to 2015 was 1600 mm and 10.2 °C, respectively, in the nearest coniferous forest weather station within 1 km from the study site, and was 1050 mm and 6.6 °C, respectively, in the nearest shrubland weather station within 1.2 km from the study site. The soils in both sites are Alfisols based on the United States Department of Agriculture (USDA) Soil Taxonomy, but with loamy sand and sandy loam surface soil textures in the coniferous forest and shrubland, respectively. The coniferous forest vegetation is dominated by *Abies fabri* (Mast.) Craib. in the canopy and *Pleurozium schreberi* Brid. Mitt. and *Rhizomnium tuomikoskii* T. Kop. in the understory bottom layer. The shrubland vegetation is dominated by *Rhododendron williamsianum* Rehd. et Wils. in the shrub canopy and *Racomitrium japonicum* Dozy et Molk in the understory bottom layer.

2.2. Experimental design and soil CO_2 emission measurement

Five plots with a size of 3 m × 3 m were established in July 2012 in each of the coniferous forest and shrubland ecosystems in a completely randomized distribution with adjacent plots within each ecosystem being at least 100 m apart. In each plot, a stainless-steel collar (0.5 m × 0.5 m) with an opaque steady-state chamber (Wang and Wang, 2003) was inserted into 8 cm below the soil surface for soil CO_2 emission measurements. These collars remained fixed throughout the study period. To minimize soil disturbance, bryophyte cover was left intact. The soil CO_2 emission from each plot was measured twice a month throughout the growing season of May to October from 2012 to 2015 except for May and June in 2012, August and October in 2013. When heavy rainfall occurred, sampling date and frequency were adjusted accordingly.

The CO_2 gas samples were collected from the headspace of the chamber (Length × Width × Height: 0.5 m × 0.5 m × 0.4 m) between 9:00 a.m. and 12:00 p.m. (Wang and Wang, 2003). The chamber was made of an aluminum frame and the sides were covered with a layer of sponge and aluminum foil to minimize temperature change inside the chamber during sampling periods. A fan was fixed on the top of the chamber to mix the gas. When sampling gas, the chamber was placed on the collar and sealed with water. A 60 mL syringe was inserted into the chamber headspace to take gas sample, and then injected into a 50 mL vacuumed gas bag. Before the next sampling of each chamber, the headspace was flushed with the air by syringe to minimize the effect of built-up concentration gradient inside the chamber. The headspace of the chamber in each plot was sampled at 0, 10, 20, and 30 min after chamber placement. The chamber was removed from the collar after sampling. The concentration of CO_2 from the chamber was analyzed with a gas chromatograph (HP 5890II, Hewlett-Packard Inc., Palo Alto, CA) equipped with a flame ionization detector. The soil CO_2 flux rate was calculated by the slope of the linear regression between CO_2 concentration and time as follows:

$$F_{CO_2} = \frac{dc}{dt} \cdot \frac{M}{V_0} \cdot \frac{P}{P_0} \cdot \frac{T_0}{T} \cdot H$$

Where F_{CO2} is the soil CO_2 flux rate; dc/dt is the concentration change rate; M is the CO_2 molar mass; P is the atmospheric pressure of the sampling site; T is the absolute temperature of the sampling time; V_0 is the molar volume (22.4 L mol^{-1}), P_0 is the atmospheric pressure (101.325 kPa), and T_0 is the absolute temperature (273.15 K) under the standard condition; H is the chamber height over soil surface.

2.3. Soil sampling and analyses

Soil samples were collected from the 0–5 and 5–15 cm soil layers from the mineral soil layer in all plots in July 2015 using a stainless-steel soil core with a 2.5 cm diameter. In each plot, four subsamples were collected randomly and thoroughly mixed to form a composite sample for each layer. Soil samples were placed in sealed plastic bags, and kept cool (< 4 °C) during transport to the laboratory. Once in the laboratory, coarse fragments and visible roots were picked from soil samples, and soils were sieved through a 2 mm mesh. A subsample of the sieved soil was air-dried at room temperature and the rest was stored in a refrigerator at 4 °C for further analysis.

The concentrations of soil organic carbon (SOC) and total nitrogen (TN) were analyzed with an elemental analyzer (CE440, Exeter Analytical Inc., North Chelmsford, MA) after the sample was ground with a ball mill to pass through a 0.15 mm sieve. The concentrations of soil dissolved organic carbon (DOC) and dissolved nitrogen (DN) were measured using a TOC/TN analyzer (Multi N/C®2100(S), Analytik Jena AG, Jena, Germany). Soil microbial biomass C (MBC) was measured by the chloroform fumigation-extraction method (Vance et al., 1987). All soil properties were presented on oven-dry basis.

2.4. Climatic data and environmental variables

The precipitation and air temperature in the coniferous forest and shrubland sites were monitored by the weather stations located at about 3000 m.a.s.l. within 1 km from the coniferous forest site and at about 3550 m.a.s.l within 1.2 km from the shrubland site, respectively.

Soil temperature at the ground surface (T_{ground}) and at 5 cm below the soil surface (T_{5cm}) were measured using a digital thermometer (JM624, Tianjin Jinming Instrument Ltd., Tianjin, China) when sampling gas. Soil water content at 5 cm below the soil surface (SWC_{5cm}) was measured with a hand-held soil moisture sensor (ML2x, Delta-T Devices, Cambridge, UK). Soil water content was not measured in 2012 due to device failure.

2.5. Statistical analyses

The mean growing-season soil CO_2 flux rate, T_{5cm} and SWC_{5cm} for each ecosystem type within the same sampling year was calculated by averaging corresponding values during the whole growing season of the year. A two-way analysis of variance (ANOVA) was conducted to test effects of ecosystem type, sampling year and their interaction on soil CO_2 emission, T_{5cm}, SWC_{5cm}, soil SOC, TN, DOC, DN, MBC and C/N. For each ecosystem type, if the interaction between ecosystem type and sampling year was not significant, a one-way ANOVA was used to determine the significance of differences among different sampling years within the subalpine coniferous forest or shrubland ecosystem, and a T-test was used to evaluate the significance of differences between the subalpine coniferous forest and shrubland ecosystems in the same sampling year. If the interaction was significant, the 'slice' function was used to determine the significance of differences by ecosystem type or sampling year at a specific level of the other treatment. A repeated measure ANOVA was conducted to test effects of ecosystem type, sampling month and their interaction on soil CO_2 emission from 2012 to 2015 using the sampling month as a repeated variable. Tukey's multiple comparison was used as the post hoc test to detect significant differences at $\alpha < 0.05$. Prior to the ANOVA or T-test, the data were examined to determine if they meet the assumptions of normal distribution and homogeneous variance.

A regression analysis was conducted to determine the relationship between soil CO_2 emission and T_{ground}, or T_{5cm} using the following exponential model:

$$F_{CO_2} = ae^{bTsoil}$$

Where a and b are the fitted parameters; Tsoil is the soil temperature at the ground surface or at 5 cm below the soil surface. The temperature sensitivity (Q_{10}) of soil CO_2 emission to changes of Tsoil was calculated as following: $Q_{10} = e^{10b}$. The relationship between soil CO_2 emission and other soil properties, such as SWC_{5cm}, soil DOC and DN was analyzed using the linear model. All statistical analyses were conducted with the SAS software (SAS 9.2, SAS Institute Inc., Cary, NC).

3. Results

3.1. Air temperature and precipitation from 2012 to 2015

There were significant variations of the mean monthly air temperature and precipitation for the four years from 2012 to 2015 in both the subalpine coniferous forest and shrubland sites (Fig. 1). The mean monthly air temperatures were higher in the forest than in the shrubland site from 2012 to 2015, with greater difference in the growing seasons than in the non-growing seasons. No differences in the mean growing-season air temperature existed during the four years for both ecosystem types, while the mean growing-season air temperatures were 3–4 °C higher in the forest than in the shrubland site from 2012 to 2015 (Fig. S1a). The annual precipitation was higher in the forest than the shrubland site from 2012 to 2015, and more than 70% of the precipitation distributed in the growing season in both ecosystems (Fig. 1). The monthly precipitation was higher in the forest than the shrubland site from April to October in all the four years. Especially in some months during the growing season, the monthly precipitation in the forest was up to twice of that in the shrubland site. The total growing-season precipitation was higher in 2012 and 2013 than in 2014 and 2015 in the forest, while it was only higher in 2013 than in 2012, 2014 and 2015 in the shrubland (Fig. S1b).

3.2. Soil CO_2 emission from the subalpine coniferous forest and shrubland

The growing-season soil CO_2 flux rate showed significant monthly variations (Fig. 2). The growing-season soil CO_2 flux rate ranged from 153.3 to 683.6 mg m^{-2} h^{-1} in the subalpine coniferous forest, which was the highest at the end of June and in the middle of September. However, the growing-season soil CO_2 flux rate ranged from 76.6 to 347.3 mg m^{-2} h^{-1} in the subalpine shrubland, which was only about half of that in the forest but had the same trend as in the forest. The ecosystem type and sampling year had significant effects on soil CO_2 flux rate, but their interaction was not significant (Table 1). There was also a significant effect of sampling month on soil CO_2 flux rate in all the four sampling years (Table 2). When averaging soil CO_2 flux rates during the whole growing season of the year, the soil CO_2 flux rate in the forest was twice as high as in the shrubland across the four years from 2012 to 2015 (Fig. 3). There was a significant difference in the mean growing-season soil CO_2 flux rate among the four years in the forest, in which it was higher in 2014 and 2015 than in 2012 and 2013 with no difference between 2014 and 2015 or 2012 and 2013, while no change was detected in the shrubland (Fig. 3).

3.3. Soil temperature and water content from 2012 to 2015

The T_{5cm} was significantly higher in the subalpine coniferous forest than the shrubland in both 2014 and 2015 (Fig. 4a). The T_{5cm} was lower in 2012 and 2013 than in 2014 and 2015 in the forest, whereas there was no such difference observed in the shrubland during the four years. The SWC_{5cm} was about 10% higher in the subalpine forest compared to that in the shrubland across the three years (Fig. 4b). However, there was no difference of SWC_{5cm} for all the three years from 2013 to 2015 for both ecosystem types.

3.4. Soil carbon and nitrogen in the subalpine coniferous forest and shrubland

Soil C and N concentrations were significantly different between the subalpine forest and shrubland for both the 0–5 and 5–15 cm soil layers (Fig. 5). The concentrations of soil SOC, TN, DOC, DN and MBC in the forest were approximately 10 times higher than those in the shrubland in the 0–5 cm soil layer. In the 5–15 cm soil layer, the concentrations of soil SOC, TN, DOC, DN and MBC in the forest were higher than those in the shrubland as well. However, there was no difference of C/N ratio between the subalpine coniferous forest and shrubland, regardless of soil layers. In the coniferous forest, the concentrations of soil SOC, TN, DOC, DN and MBC were 5–10 times higher in the 0–5 cm than in the 5–15 cm soil layer, while there was only slight decrease in the concentrations of soil SOC, TN, DOC, DN and MBC from the 0–5 to the 5–15 cm soil layer in the shrubland.

3.5. Relationship between soil CO_2 emission and soil properties in the subalpine coniferous forest and shrubland

Relationships between soil CO_2 flux rate and soil temperature varied depending on the soil depth at which soil temperature was measured (Fig. 6). There was no significant relationship between soil CO_2 flux rate and the T_{ground} (Fig. 6a), however, the soil CO_2 flux rate was

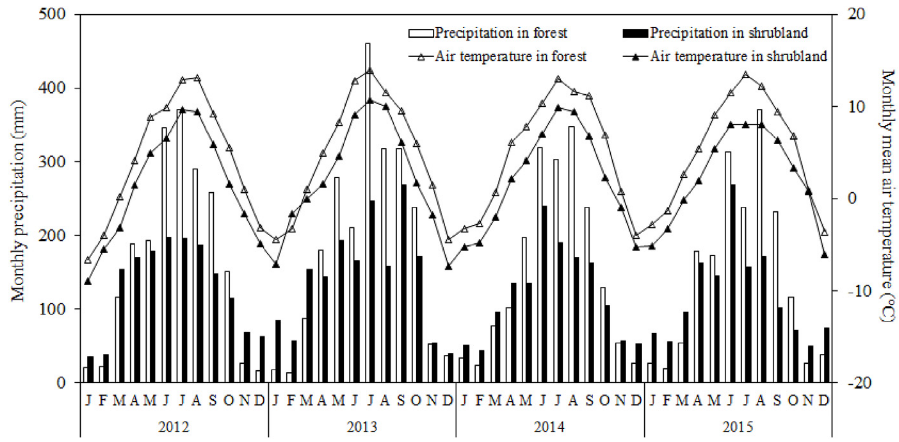

Fig. 1. Mean monthly air temperature and precipitation from 2012 to 2015 in the subalpine coniferous forest and shrubland.

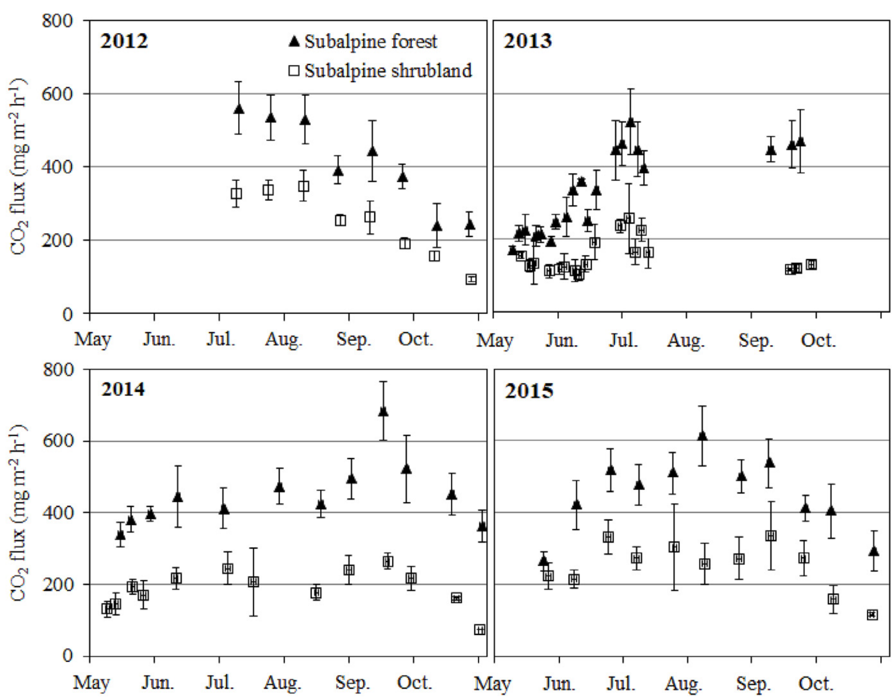

Fig. 2. Soil CO_2 flux rates during the growing season from 2012 to 2015 in the subalpine coniferous forest and shrubland. Vertical bars are standard errors of means (n = 5).

Table 1
F-statistics of two-way ANOVA for effects of different ecosystem type (the coniferous forest and shrubland), sampling year (from 2012 to 2015), and their interaction on soil CO_2 emissions.

Source of variation	df	F	*p*
Ecosystem type	1	83.5	< 0.001
Sampling year	3	19.1	0.024
Ecosystem type × Sampling year	3	2.6	0.316

exponentially related to the T_{5cm} (Fig. 6b). When separating the soil CO_2 flux rates in the subalpine coniferous forest from those in the shrubland, approximately 48% of the variation in soil CO_2 flux rate could be explained by the T_{5cm} in the forest and approximately 35% of the variation could be explained by the T_{5cm} in the shrubland (Fig. 7). Both subalpine forest and shrubland had the same Q_{10} of 3.67. There was positive relationship between the soil CO_2 flux rate and the SWC_{5cm}, and approximately 16% of the variation in soil CO_2 flux rate could be explained by the SWC_{5cm} (Fig. 6c). Meanwhile, the soil CO_2 flux rate was positively related to the soil DOC or DN concentration in the subalpine coniferous forest and shrubland (R^2 = 0.46 for DOC and R^2 = 0.48 for DN, Fig. 8).

4. Discussion

The subalpine coniferous forest had a growing-season soil CO_2 flux rate of about twice of that in the subalpine shrubland in the same period, reflecting effects of vegetation type on soil CO_2 emission. Our previous investigation indicated that the coniferous forest relative to the shrubland has a higher SOC and DOC content (Sun et al., 2017), which along with the higher soil temperature and water content in the coniferous forest (Fig. 4) explained well the differences of soil CO_2 flux rate between the two subalpine ecosystems. The mean growing-season soil CO_2 flux rates in the coniferous forest (322.6–423.1 $mg\,m^{-2}\,h^{-1}$ from 2012 to 2015) fell in the range of those reported by other studies in coniferous forests in different regions (Swanson and Flanagan, 2001; Botting and Fredeen, 2006; Chen et al., 2014; Berryman et al., 2016), but were lower than those reported by Pang et al. (2016) with estimated

Table 2
F-statistics of the repeated measure ANOVA for effects of different ecosystem type (the coniferous forest and shrubland), sampling month (from May to October), and their interaction on soil CO_2 emissions in sampling years from 2012 to 2015.

Sampling year	Source of variation	df	F	*p*
2012	Ecosystem type	1	34.7	< 0.001
	Sampling month[a]	3	41.3	0.002
	Ecosystem type × Sampling month	3	1.3	0.513
2013	Ecosystem type	1	21.8	< 0.001
	Sampling month[a]	3	18.3	0.026
	Ecosystem type × Sampling month	3	2.7	0.204
2014	Ecosystem type	1	11.2	< 0.001
	Sampling month	5	4.3	0.035
	Ecosystem type × Sampling month	5	1.9	0.422
2015	Ecosystem type	1	15.6	< 0.001
	Sampling month	5	8.7	0.030
	Ecosystem type × Sampling month	5	2.0	0.387

[a] The soil CO_2 emission was not measured in May and June of 2012, August and October of 2013.

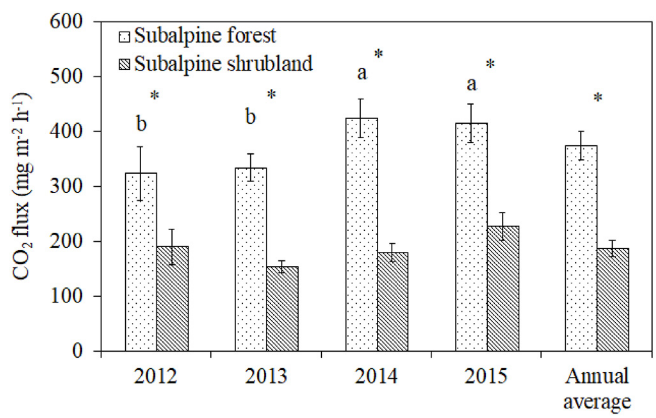

Fig. 3. Mean growing-season soil CO_2 flux rates in the subalpine coniferous forest and shrubland from 2012 to 2015. Different letters represent significant differences ($p < 0.05$) among different sampling years for each ecosystem type. Asterisks represent significant differences ($p < 0.05$) between the subalpine coniferous forest and shrubland in the same sampling year. Vertical bars are standard errors of means (n = 5).

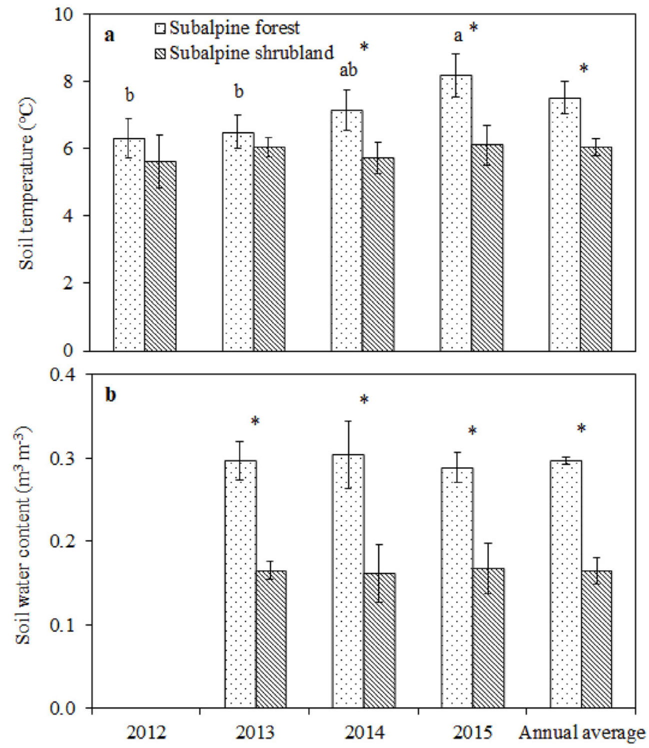

Fig. 4. (a) Mean soil temperature and (b) soil water content at 5 cm below the soil surface in the subalpine coniferous forest and shrubland during the growing season from 2012 to 2015. Different letters represent significant differences ($p < 0.05$) among different sampling years for each ecosystem type. Asterisks represent significant differences ($p < 0.05$) between the subalpine coniferous forest and shrubland in the same sampling year. Vertical bars are standard errors of means (n = 5).

soil CO_2 flux rate of 443.5 mg m^{-2} h^{-1} in a Minjiang Fir (*Abies faxoniana*) and spruce (*Picea asperata*) dominated subalpine forest in China and by Berryman et al. (2015) with the soil CO_2 flux rate ranging from 660.0 to 880.0 mg m^{-2} h^{-1} in a lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa*) dominated high elevation forest in Colorado's Rocky Mountains under very similar environmental condition as in this study. We speculate that the lower soil CO_2 flux rate in this study might be attributed to lower leaf and root litter input to the soil or different terrains of forest sites. The mean growing-season soil CO_2 flux rates in the subalpine shrubland (152.4–225.8 mg m^{-2} h^{-1} from 2012 to 2015) were several times higher than those in an alpine tundra (60.1–82.1 mg m^{-2} h^{-1}) dominated by dwarf shrubs of *Dryas octopetala* var. *asiatica*, *Vaccinium uliginosum* and *Rhododendron aureum* at the Changbai Mountain in China (Zhou et al., 2016), but were lower than those reported by Imer et al. (2013) in an alpine grassland in Switzerland. The differences could be attributed to lower mean annual temperature in the alpine tundra (Zhou et al., 2016), and higher SOM input in the alpine grassland (Imer et al., 2013). Moreover, it is worth to note that the soil CO_2 emissions were measured in plots with bryophytes in both subalpine forest and shrubland sites in this study. According to Sun et al. (2017), the bryophyte respiration accounted for 6–15% of the total floor CO_2 emission in subalpine ecosystems. Swanson and Flanagan (2001) and Gaumont-Guay et al. (2008) also observed that a small fraction of the total soil CO_2 emission was released from the bryophyte respiration in a feather moss dominated boreal black spruce forest. Thus, the soil CO_2 flux rates may be overestimated in this study.

Contrasting to the amount difference of soil CO_2 emission between the two ecosystems, the monthly variation of soil CO_2 emission exhibited a similar trend, which followed the variation of the mean monthly air temperature and the monthly precipitation, i.e., soil CO_2 emission increased as the increase of the mean monthly air temperature and the monthly precipitation in both ecosystems. Those results were in line with many previous studies that air temperature and precipitation contributed to CO_2 emission in different terrestrial ecosystems (Raich and Schlesinger, 1992; Raich et al., 2002; Li et al., 2016; Baldocchi et al., 2018). Moreover, the significant inter-annual variation of soil CO_2 emission from the subalpine forest was surprisingly not associated with the variation of the mean growing-season air temperature, but opposite to the variation of the total growing-season precipitation. When exploring the variation of soil water content, we found that there was no difference even if the total growing-season precipitation in 2012 and 2013 was higher than that in 2014 and 2015 in the forest. The reason was not clear. We speculate that it could be attributed to the loamy sand soil texture with low water holding capacity in the forest site. Although there was significant inter-annual variation of the total growing-season precipitation from 2012 to 2015, no changes of the mean growing-season air temperature resulted in the non-significant inter-annual variation of soil CO_2 emission from the subalpine shrubland. This indicates that air temperature has greater influence than precipitation on soil CO_2 emissions in the subalpine shrubland ecosystem.

Soil CO_2 emission is very complex as it involves diverse soil

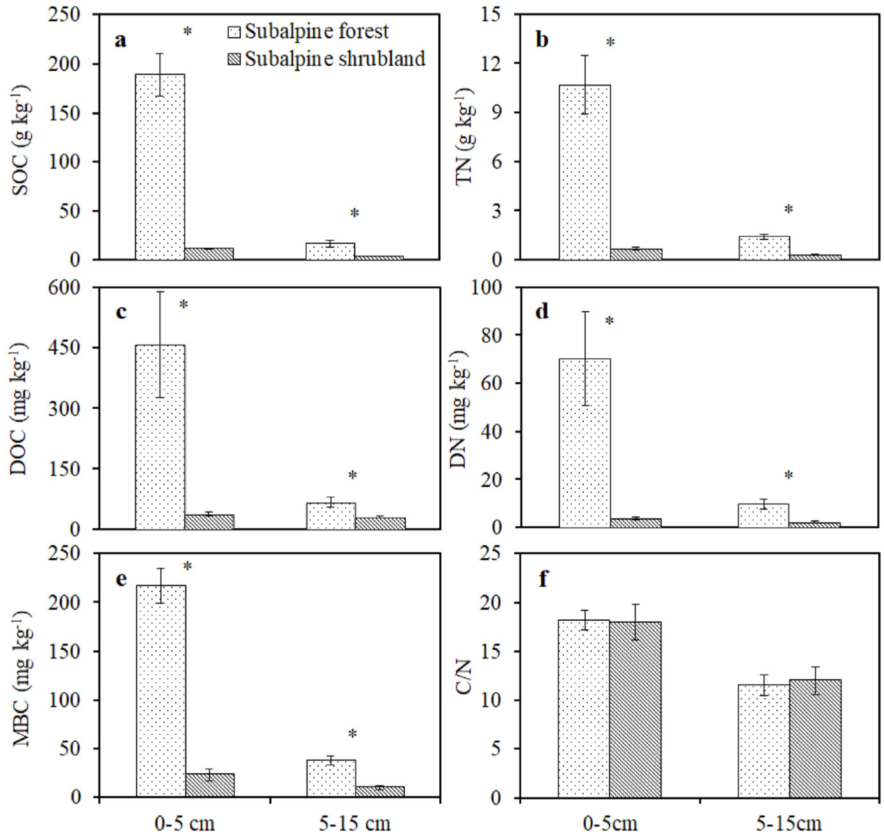

Fig. 5. Soil (a) organic carbon, (b) total nitrogen, (c) dissolved organic carbon, (d) dissolved nitrogen, (e) microbial biomass carbon, and (f) carbon to nitrogen ratio in 0–5 and 5–15 cm soil layers in the subalpine coniferous forest and shrubland. Asterisks represent significant differences (p < 0.05) between the subalpine coniferous forest and shrubland in the same soil layer. Vertical bars are standard errors of means (n = 5).

biochemical processes, plant communities, soil microbes, as well as abiotic conditions (Ryan and Law, 2005). Changes in biophysical factors, such as soil temperature (Lloyd and Taylor, 1994), soil moisture (Davidson et al., 1998), vegetation property (Imer et al., 2013; Chen et al., 2014), microbial activity and community structure (Zhang and Zak, 1998), root biomass (Tang et al., 2005; Luan et al., 2012), and belowground C allocation (Ryan and Law, 2005) can alone or in combination influence soil CO_2 flux to the atmosphere (Ryan and Law, 2005; Gaumont-Guay et al., 2008). In this study, the close positive relationship between CO_2 emission and soil temperature (R^2 = 0.45, p < 0.001) and between CO_2 emission and soil water content (R^2 = 0.16, p < 0.001), and the higher soil CO_2 flux rate and soil temperature and water content in the subalpine coniferous forest than in the shrubland support our hypothesis that the lower soil CO_2 flux rate in the subalpine shrubland compared with that in the subalpine forest was mainly attributed to lower soil temperature and water content induced by higher elevation in the subalpine shrubland. This was in line with findings in many other ecosystems (Lloyd and Taylor, 1994; Wang

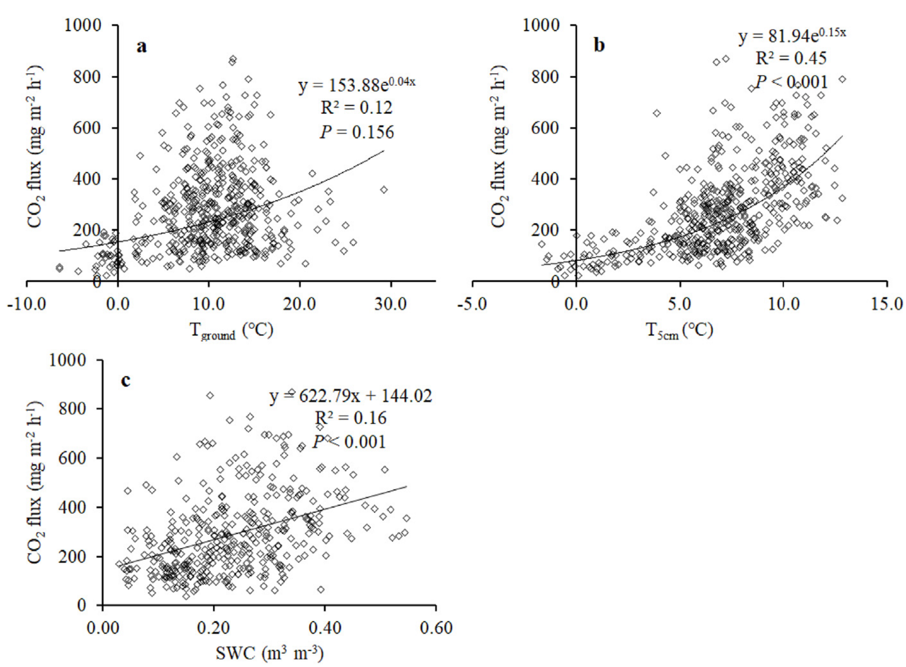

Fig. 6. Relationships between (a) soil CO_2 flux rate and soil temperature at the ground surface (T_{ground}), between (b) soil CO_2 flux rate and soil temperature at 5 cm below the soil surface (T_{5cm}), between (c) soil CO_2 flux rate and soil water content at 5 cm below the soil surface (SWC_{5cm}) in the subalpine coniferous forest and shrubland.

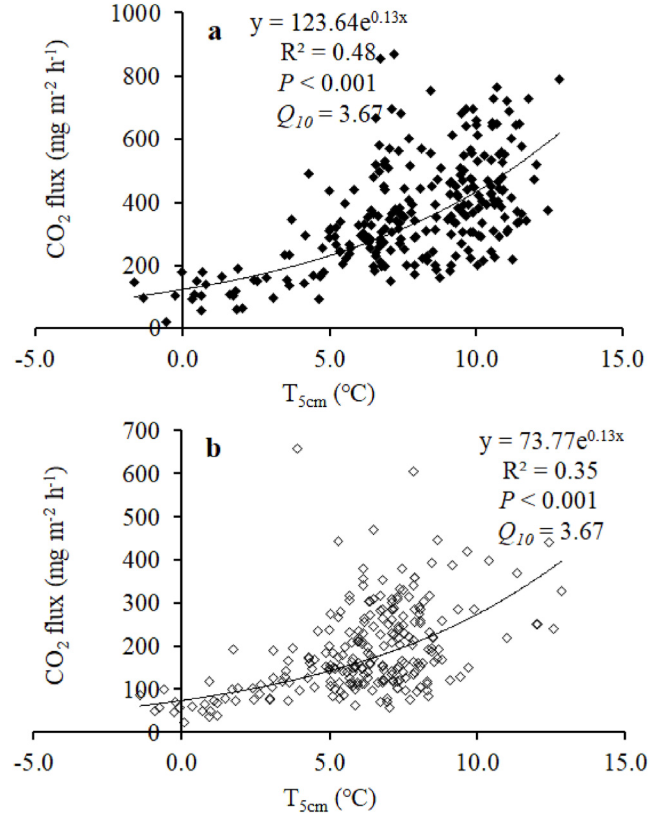

Fig. 7. Relationships between soil CO_2 flux rates and soil temperature at 5 cm below the soil surface (T_{5cm}) (a) in the subalpine coniferous forest and (b) shrubland, respectively.

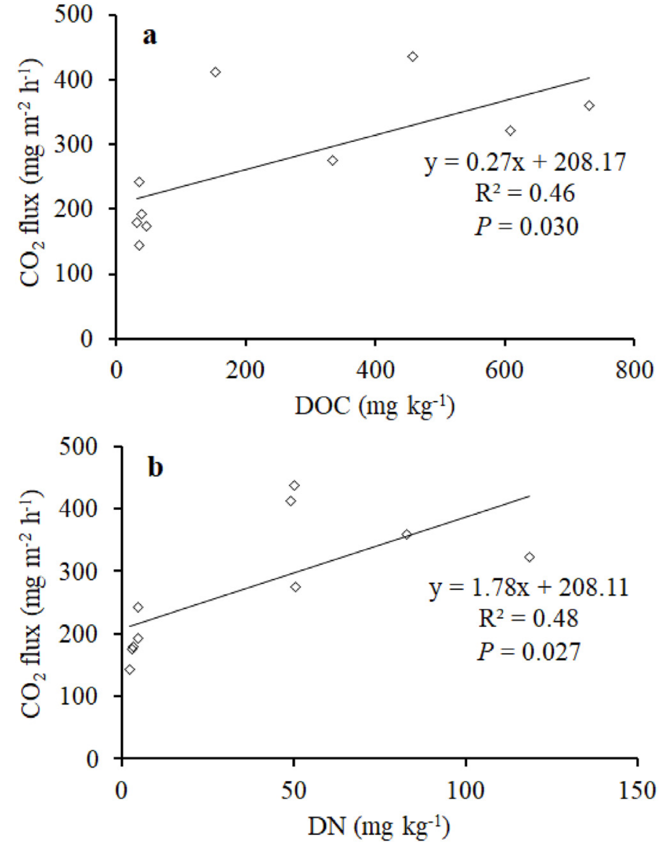

Fig. 8. Relationships between (a) soil CO_2 flux rates and soil dissolved organic carbon (DOC), between (b) soil CO_2 flux rate and soil dissolved nitrogen (DN) in the subalpine coniferous forest and shrubland.

et al., 2006; Laganière et al., 2012; Chen et al., 2016). Higher soil temperature and water content increased soil microbial biomass and activity, enhanced litter decomposition and soil heterotrophic respiration and rhizospheric respiration (Kirschbaum, 1995; Lu and Cheng, 2009; Xu et al., 2013; Pang et al., 2016). Davidson et al. (2006) also reported that soil temperature and water content could affect soil enzyme activity and the affinity of enzyme for substrates, thus regulating substrate decomposition. Besides the contribution of soil temperature and water content to soil CO_2 emission, the positive relationship between soil CO_2 flux rate and soil DOC or DN concentration in both ecosystems in this study suggests that soil C and N pools, especially the labile C pool in the soil, were also controlling factors for soil CO_2 emission in subalpine ecosystems. Previous studies showed that SOM, microbial biomass and aboveground and belowground biomass all directly or indirectly influenced soil C and N pools, which could provide substrates for soil heterotrophic respiration (Ryan and Law, 2005; Wang et al., 2006; Pang et al., 2016).

The SOM was mainly derived from litter fall, root litter and microbes. The quantity and quality of SOM affected SOM decomposition, thus determining soil CO_2 flux rate (Ryan and Law, 2005; Laganière et al., 2012; Pang et al., 2016). Studies showed that high amount of tree and root biomass benefited for the accumulation of leaf and root litter, favoring SOM formation (Kögel-Knabner, 2002; Potthast et al., 2010). In this study, the subalpine forest was expected to have a greater tree and root biomass than shrubland, which could guarantee a greater quantity of litter input and SOM. This was supported by the higher SOC and TN concentrations in the subalpine forest than shrubland. Moreover, microbial residue was another important input to SOM (Kögel-Knabner, 2002). The higher soil microbial biomass C in the subalpine forest than shrubland in this study indicates the greater labile C input into SOM, which will benefit for the SOM decomposition.

Soil microorganisms, as the key components of belowground ecosystems, differed in their capability to use SOM. Greater soil labile C could result in a more biologically-active system (Budge et al., 2011), which increased CO_2 release from the soil (Laganière et al., 2012), while greater soil recalcitrant C restricted microbial utilization, thus decreasing soil CO_2 emission. Studies showed that the litter of coniferous trees had high lignin concentration, which was considered as a recalcitrant OM (Landsberg and Gower, 1997). Meanwhile, shrub litter, particularly *Ericaceae*, also had high concentration of lignin and low concentration of cellulose, thus decreasing the SOM decomposability (Budge et al., 2011). Therefore, the quality of SOM in the subalpine forest was not too much different from that in the subalpine shrubland in this study. However, the higher DOC concentration in the subalpine forest than in the shrubland suggests that the forest soil could provide more labile C for microbial decomposition of SOM, thus increasing soil CO_2 release. Moreover, microbial heterotrophic respiration accounted for an important proportion of soil respiration (Ryan and Law, 2005). The higher soil microbial biomass C in the subalpine forest than shrubland in this study also indicates greater microbial activity and higher microbial respiration, which contributed to the higher soil CO_2 emission in the subalpine forest compared with the shrubland.

Root respiration played an important role in regulating soil respiration (Ryan and Law, 2005; Tang et al., 2005). Raich and Schlesinger (1992) reviewed soil respiration rate from the global terrestrial and wetland ecosystems and estimated that root respiration accounted for at least 24% of total soil respiration. Different plant species were associated with different root biomass, morphology and physiology, which could affect the contribution of root respiration to total soil respiration (Hobbie, 1996; Wang et al., 2006; Phillips et al., 2012; Chen et al., 2016; Pang et al., 2016). Wang et al. (2006) compared soil respiration in six temperate forests in China, and found that the soil respiration in the evergreen pine plantation was significantly

higher than that in the deciduous larch plantation due to more root biomass in the pine forest, which resulted in more than 2.5 times higher root respiration, rather than the heterotrophic respiration. In this study, we speculate that the subalpine *A. fabri* forest could have higher fine root biomass than the subalpine *R. williamsianum* shrubland, which might also contribute to the higher soil CO_2 flux rates in the forest than the shrubland. Meanwhile, root exudates associated with plant species could indirectly modify SOM decomposition by influencing soil microbial community, biomass and activity due to different nutrient demands of microbes (Grayston and Prescott, 2005; Mitchell et al., 2010; Ushio et al., 2010). This also could be a potential reason for the differences in soil CO_2 emission between different subalpine ecosystems in this study.

Different ecosystems respond to climate change differently. High altitude regions are assumed to be very sensitive and vulnerable to climate change due to severe temperature limitations (Fu et al., 2006; Budge et al., 2011; Zhou et al., 2016). Globally, the temperature sensitivity of soil CO_2 emission was estimated to be 1.5 (Bond-Lamberty and Thomson, 2010), and it increased with decreasing soil temperature (Schindlbacher et al., 2010). The higher Q_{10} in both subalpine forest and shrubland in this study than the global average Q_{10} suggests that high elevation soils will be more responsive to global warming, and they will be affected in a more sensitive temperature range than their low elevation counterparts. Generally, subalpine and alpine species are well adjusted to low temperature (Germino and Smith, 2000). A similar level of temperature increase could result in more significant impacts on high elevation compared to low elevation species (Lloyd and Taylor, 1994; Pepin et al., 2015). The subalpine shrubland is expected to respond more readily to temperature increase; however, the same temperature sensitivity of soil CO_2 emission between the subalpine forest and shrubland in this study (Q_{10} of 3.67) indicates that they may not respond differently to global warming without taking into account changes in precipitation patterns and vegetation succession induced by global warming. IPCC (2013) projected that global temperature would increase by 0.6 °C over the 21st century in higher altitude and latitude ecosystems. Temperature increase will affect biogeochemical processes, especially the ecosystem C balance, in alpine and subalpine ecosystems (Schlesinger and Andrews, 2000; Bond-Lamberty and Thomson, 2010; Budge et al., 2011). Because of significant amount of soil CO_2 emission in alpine and subalpine ecosystems and the uncertainty in future climate change, long-term measurements and further analyses of CO_2 dynamics are needed to understand and predict the response of terrestrial C cycling in those ecosystems to global climate change.

5. Conclusions

The subalpine coniferous forest soil demonstrated a great level of monthly and inter-annual variations in CO_2 emission, while less inter-annual variation was found in the subalpine shrubland soil. Soil CO_2 flux rates in the subalpine shrubland were only half of those observed in the subalpine coniferous forest during the growing season. The higher soil CO_2 flux rates in the coniferous forest relative to the shrubland were attributed to the elevation-induced higher soil temperature and water content and the vegetation-induced higher soil C and N pools in the coniferous forest ecosystem. The same temperature sensitivity of soil CO_2 emission between the subalpine forest and shrubland indicates that they will not respond to global warming differently without considering precipitation pattern change and vegetation succession induced by global warming. Our results help elucidate differences in soil CO_2 emission between different subalpine ecosystems and provide a more reasonable estimation of soil CO_2 emission from subalpine ecosystems on the Qinghai-Tibetan Plateau. These empiric results are important in developing and testing models used to predict ecosystem C dynamics in a changing climate.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.atmosenv.2018.10.067.

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